Evidence of character displacement in microhabitat use between two tropical sympatric *Holcosus* lizard species (Reptilia, Teiidae)

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Abstract

Evidence of character displacement in microhabitat use between two tropical sympatric Holcosus *lizard species (Reptilia, Teiidae).* Interspecific competition between sympatric related species leading to character displacement is critical for species coexistence, especially in tropical habitats. We examined microhabitat use of two sympatric species of tropical lizards of the genus *Holcosus* in relationship to the microhabitats available in two ecosystems. The species *H. festivus* lives exclusively in the forest and uses microhabitats in proportion to their availability; while the other, *H. quadrilineatus,* lives both in forest and on the beach and selects microhabitats with specific characteristics. In the ecosystem where these two lizards live in sympatry (forest), we observed a differential microhabitat use between the two species. However, these differences indicated changes in habitat use by *H. quadrilineatus* (the smaller species) concerning its patterns of habitat selection in the ecosystem (beach) where only this species occurs. The age of the lizards did not affect the patterns of selection of microhabitats of either species. Shifts in microhabitat use may allow coexistence in sympatry of both species, which might result from the competitive exclusion of the smaller species by the larger species.

Key words: Interspecific competition, *Holcosus,* Lizards, Microhabitat use, Tropical habitats

Resumen

Evidencia del desplazamiento de caracteres en el uso de microhábitats entre dos especies simpátridas de lagartos tropicales del género Holcosus *(Reptilia, Teiidae).* La competencia interespecífica entre especies simpátricas relacionadas que conduce al desplazamiento de caracteres es crucial para la coexistencia de las especies, en especial en hábitats tropicales. Examinamos el uso de los microhábitats disponibles en dos ecosistemas por dos especies simpátricas de lagarto tropical del género *Holcosus*. La especie *H. festivus* vive exclusivamente en el bosque y utiliza microhábitats en proporción a su disponibilidad, mientras que la otra, *H. quadrilineatus*, vive tanto en el bosque como en la playa, y selecciona microhábitats con características específicas. En el ecosistema donde estos dos lagartos viven en simpatría (el bosque), observamos un uso diferente de microhábitats entre ambas especies. Sin embargo, estas diferencias indicaron cambios en el uso del hábitat de *H. quadrilineatus* (la especie más pequeña) con respecto a sus patrones de selección de hábitat en el ecosistema (la playa) donde solo está presente esta especie. La edad de los lagartos no afectó a los patrones de selección de microhábitat de ninguna especie. Los cambios en el uso de los microhábitats pueden permitir la coexistencia en simpatría de ambas especies, lo que podría ser consecuencia de la exclusión competitiva de la especie más pequeña por la más grande.

Palabras clave: Competencia interespecífica, *Holcosus*, Lagartos, Uso del microhábitat, Hábitats tropicales

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Introduction

Interspecific competition has an important effect driving evolutionary and ecological diversification because when two or more species undergo intense competition for similar resources such as food or habitat (Begon et al., 1996; Dhont, 2011), they can diverge by ecological character displacement (Day and Young, 2004; Stuart and Losos, 2013). Interspecific competition may be especially important in tropical habitats due to the high biodiversity of species found in sympatry with similar ecological niches. For example, many studies examining the different interspecific interactions in the structure of the community of lizards in Neotropical biomes have found evidence of competition (Vitt et al., 2000a, 2000b, Hatano et al., 2001, Rocha et al., 2009).

An assumption of the theories of competition is that the strength of between–species competition is inversely related to the amount of interspecific resource partitioning (Pacala and Roughgarden, 1982). Thus, when studying the interactions between pairs of similar species, it is necessary to quantify the degree of overlap by use of resources (Hurlbert, 1978). It has been shown that two species of sympatric lizards could coexist in the same place and time if there were a series of ecological parameters that would confer differentiating characteristics in, for example, the way of feeding, activity times, morphology, or physiology (Huey, 1979; Chase et al., 2002). However, the distinct spatial occupation on the available microhabitats within a given ecosystem is considered a critical factor determining the coexistence of sympatric species (Pianka, 1973; Schoener, 1974; Calsbeek, 20098), and it may also explain speciation processes (Losos, 2009). In addition, ontogenetic changes in size or any ecological aspect should be accounted for because these may differentially affect the intensity of potential competition, which may be age–specific (e.g., Smith 1981). Through these studies, it will be possible to determine factors that condition the life of the species, being able to approximate the impact that human activity may cause them (Böhm et al., 2013).

In many tropical forests of Central America, two similar species of lizards of the genus *Holcosus* (formerly *Ameiva*) (Family Teiidae) co–occur (Savage, 2002; Abella et al., 2008). *Holcosus festivus* (also known as the Middle American ameiva or tiger ameiva) is a large lizard that reaches a total length of 34.5 cm. It inhabits mainly forest areas, with higher activity at midmorning on sunny days. *Holcosus quadrilineatus* (the four–lined ameiva) is smaller, reaching a total length of 28.3 cm, and it is found in open areas, forest margins and in clearings, where it is more active in the morning (Savage, 2002). Information on the ecology of these two species of lizards focuses on their temperature preferences (Hirth, 1965), thermoregulation and activity patterns (Vitt and Zani, 1996; Sebastián–González and Gómez, 2012), reproduction (Smith, 1968a, 1968b; Fitch, 1973), parasitology (Bursey et al., 2006), escape responses (Lattanzio, 2014), diet (Hirth, 1963; Whitfield and Donnelly, 2006), and other more general ecological aspects (Hirth, 1963; Hillman, 1969; Fitch, 1973; Vitt and Zani, 1996). However, few studies are examining the possible competitive interactions between the two species (Sebastián–González and Gómez, 2012).

Here, we investigate the partition of microhabitats between these two lizard species (*H. festivus* and *H. quadrilineatus*) relative to their availability and analyze whether ecological displacement to avoid interspecific competition may explain their coexistence in the same areas. We estimated the degree of overlap or ecological distribution in terms of microhabitat use between these two species that inhabit the same area (Pacuare Natural Reserve, Costa Rica). *Holcosus quadrilineatus* occupies two types of ecosystems (beach and forest) (fig. 1), whereas *H. festivus* occurs only in the forest area. We determined the structural characteristics of the microhabitats occupied by each species in the two types of ecosystems in relation to the microhabitats available in each area. Specifically, we aimed to determine: (1) whether there was a selection of specific microhabitats with respect to those available, or whether the habitat was simply used as a function of its availability; (2) whether there was a differential microhabitat use between species in those areas where they were sympatric; and (3) if there were such differences, whether this implied changes in habitat use with respect to the patterns of habitat selection in the areas where only one of the species was found. Finally, we examined (4) the effect of age on these patterns of habitat use and the possible competitive interactions between species.

Material and methods

Study area

The study was performed in the Pacuare Natural Reserve, Costa Rica (10º 13' 50'' N / 83º 16' 72'' W to the north, 10º 12' 50'' N / 83º 3' 22'' W to the south). The Reserve comprises 800 ha of rainy secondary forest and swampy areas, surrounded by the Tortuguero channel system and the Caribbean Sea. More than 300 vertebrate species, including 52 reptile species, are found in the reserve. There are two research stations, a northern station and a southern station joined by a path system (Abella et al., 2008).

The Reserve has two ecosystems: (1) a rainy secondary forest (fig. 1A); and (2) a beach area with a volcanic sand substrate (fig. 1B), located in the southern station. Therefore, the observations were divided according to the type of ecosystem (forest vs beach). In this reserve, only one study on thermoregulation and activity patterns of these *Holcosus* lizard species has been performed (Sebastián–González and Gómez, 2012), so knowing more about their ecology will allow improvement in the management and conservation of these species in the environment of the reserve.

Data sampling

The study was carried out at the beginning of the rainy season, during 15 days of May 2017. The reserve is divided by several trails: a main trail that connects the

Fig. 1. Views of the two main ecosystems, a) forest and b) beach, used by *Holcosus* lizards in the study area.

Fig. 1. Vista de los dos principales ecosistemas, a) el bosque y b) la playa, utilizados por los lagartos del género Holcosus *en la zona de estudio.*

southern station with the northern station, and several secondary trails. Every day, if the weather favored lizard activity, we slowly walked the trail system of the reserve looking for lizards during their hourly peaks of higher activity (morning: 06.30–09.00 h; midday: 10.00–12.30 h; afternoon: 15:00–17.00 h) (Savage, 2002). Surveys covered the beach area, and three sections of the forest, with a similar search effort in all the areas. The surveys followed trails that were repeated on different days, so there could be a potential repetition in the sighting of the same individual lizards. However, given that the abundance of lizards was high, and since we avoided repeating sampling in a specific area (a minimum distance of 4 m between observations was established), we are confident that the probability of repeated observations of the same individuals was low and did not affect the results.

Every time that an individual lizard was sighted, we recorded the hour of the day and the species, and calculated the age of the individual. We distinguished adults from juveniles by their body size and morphological traits; *H. quadrilineatus* juveniles are less than 6 cm in length and *H. festivus* are less than 7–8 cm in length (Savage, 2002). Additionally, juveniles of *H. quadrilineatus* have two pairs of lateral and ventrolateral yellow stripes and blue tails (brown in adults), and juveniles of *H. festivus* have a vertebral bright blue stripe that extends from the tip of the snout almost to the tip of the tail; this changes to white or yellow with age (Savage, 2002). Then, we measured microhabitat use of the lizard by taking four transects of 2 m each, one at each of the four cardinal orientations (N, S, E, W) radiating from the point where the individual was first sighted. In each transect, the characteristics of the microhabitat were noted at four points at 50, 100, 150 and 200 cm from the central point (Martín and López, 1998). At each point, we noted the substrate type (sand, leaf litter, grass, bare soil or tree trunk). We also noted whether there was tree cover above the point, and whether sun exposure wasshade or sunny. Furthermore, we assessed the moisture content of the substrate (dry or wet). Finally, we noted the contacts of a bar placed vertically with the vegetation at heights of 5, 10, 25 and 50 cm above each point, and the type of vegetation in each contact (*Ipomoea* sp. 1, *Ipomoea* sp. 2, *Coccoloba* sp., *Hybiscus* sp., *Heliconia* sp., or Fam. Rubiaceae, Piperaceae, Cyperaceae, Gramineae or Palmae). In this way, we obtained microhabitat data for 16 points around the observation point for each lizard, allowing us to calculate the percentages of the cover of each of the 23 microhabitat variables for each observation. We obtained 83 observations of lizards (50 *H. quadrilineatus* and 33 *H. festivus*).

To study the availability of microhabitats, we used the same procedure to measure microhabitats at points (N = 35) determined at random while walking following straight line paths (a minimum distance of 4 m was established between points), in the same paths of the study area used to study lizards.

Data analyses

We performed a principal components analysis (PCA) to reduce the number of microhabitat variables (23) to a small number of principal components (PCs) that described the habitat. The original data (i.e. number of contacts with each microhabitat variable) were square–rooted to ensure that they were fitted to a normal distribution. We used analyses of variance (ANOVAs) to compare differences in the use of the different types of microhabitats described by the PCA (PC scores) between the points available in the habitat and those used by each of the species in each of the ecosystems (forest vs beach). Post–hoc tests (Tukey's tests) were used for pairwise comparisons. These analyses were carried out using the R Studio statistical software (R Core Team, 2017).

Results

Table 1 shows the average values for each of the microhabitat variables available and used by each species in each type of ecosystem (forest vs beach). The PCA performed with all microhabitat variables produced six principal components (PCs) with eigenvalues greater than 1, which together accounted for 64.4 % of the explained variance (table 2). The first component (PC1) represented a gradient from microhabitats with high cover of sand to areas with high cover of leaf litter. The second component (PC2) described a gradient from microhabitats with high grass cover to areas with high cover of tall (50 cm) bush vegetation. The third component (PC3) represented a gradient from dry to humid substrates. The fourth component (PC4) represented a gradient toward microhabitats with high cover of bush vegetation of 25 cm in height above the ground. The fifth component (PC5) described a gradient towards microhabitats with palms and the presence of tree trunks at the substrate level. Finally, the sixth component (PC6) represented a gradient from areas with high cover of *Hybiscus* sp. to areas with high cover of gramineous herbs. There were significant differences between groups (microhabitats available and used by each species in each type of ecosystem) in most PCs, except in the case of PC4 and PC5 (table 2).

Regarding the PC1 (fig. 2A), *H. quadrilineatus* inhabiting beaches selected microhabitats with less leaf litter than expected given the average availability of leaf litter in the beach environment (Tukey's test, $p = 0.0045$). Also in the forest, although leaf litter was significantly more abundant here than on the beach ($p < 0.0001$), *H. quadrilineatus* selected substrates with significantly less leaf litter than what was available on average ($p = 0.002$). However, in the forest, *H. quadrilineatus* used microhabitats with significantly more leaf litter than those used by this species on the beach ($p < 0.0001$). In contrast, *H. festivus* used leaf litter in proportion to its availability in the forest ($p = 0.92$). This pattern resulted in significant differences between the two lizard species in the use of these substrates within the forest ($p < 0.008$), with *H. festivus* using microhabitats with more leaf litter than *H. quadrilineatus*.

In relation to the PC2 (fig. 2B), *H. quadrilineatus* on the beach used microhabitats with grass or tall bushes according to what was expected given their availability (Tukey's test, $p = 0.96$). However, in the forest, although the availability of grass and tall bushes was similar to that on the beach ($p = 0.28$), *H. quadrilineatus* selected microhabitats with significantly much more grass cover and fewer bushes than what was available on average ($p < 0.0001$). Therefore, *H. quadrilineatus* used microhabitats with significantly more grass and fewer tall bushes in the forest than on the beach ($p < 0.0001$). In contrast, *H. festivus* used microhabitats with grass and bushes in the forest in proportion to their availability ($p = 0.91$). Between the two species, there were significant differences in the forest ($p < 0.0001$); *H. quadrilineatus* selected microhabitats with significantly more grass cover and fewer tall bushes than those used by *H. festivus*.

Regarding the PC3 (fig. 2C), on the beach *H. quadrilineatus* used substrates with humidity levels similar to those available on average in the environment (Tukey's test, $p = 0.22$). However, in the forest, this species used substrates that were significantly dryer than those available on average ($p = 0.002$). Therefore, *H. quadrilineatus* shifted its use of microhabitats depending on the ecosystem, using significantly more dry substrates in the forest than on the beach ($p = 0.025$) even though the average humidity of available substrates was significantly higher in the forest than on the beach ($p = 0.04$). *H. festivus*, on the other hand, used substrates with humidity levels similar to those available on average in the forest ($p = 0.29$). However, there were no significant interspecific differences in the use of substrates in relationship to their humidity within the forest ($p = 0.19$).

For PC4 (fig. 2D) and PC5 (fig. 2E), there were no significant differences between groups. Thus, these variables (PC4, contact with vegetation at 25 cm; PC5, palms and tree trunks) did not seem to affect microhabitat selection and both species used them in proportion to availability in both ecosystems.

In the case of PC6 (fig. 2F), both species used what was available in the environment (Tukey's tests, *H. quadrilineatus*: beach $p = 0.13$, forest $p = 0.62$, *H. festivus*: forest $p = 0.18$), which did not significantly differ between forest and beach ($p = 0.97$). Thus, there were no significant differences between species in the use of microhabitats with *Hybiscus* sp. or gramineous herbs within the forest ($p = 0.94$).

Habitat use according to age classes

After partitioning the observations according to the age of the lizards (juvenile vs adult), there were no significant differences between ages, within each species and habitat, in the use of microhabitats defined by any of the PCs (Tukey's tests, $p > 0.40$ in all between ages comparisons). That is, both juveniles and adults of the same species followed the same patterns of microhabitat use within each ecosystem. This result indicated that age did not affect the selection of microhabitats of each species, and therefore, age should not influence the possible competition between species.

Discussion

Considering the results of the availability and use of the microhabitats, we found that the two *Holcosus* lizard species differed in their general strategies of microhabitat use. While *H. festivus*, which was found only in the forest, used different microhabitats according to what was expected given their availability, *H. quadrilineatus* showed in many cases a distinct use of microhabitats relative to their availability. Thus, microhabitat variables such as leaf litter and grass cover, tall bushes and substrate humidity levels seem to affect the use of microhabitat by *H. quadrilineatus*.

Table 1. Variables (mean ± SE) that characterize the microhabitats available and used by *H. quadrileneatus* (Hq) and *H. festivus* (Hf) lizards in two types of ecosystems (beach and forest).

Tabla 1. Variables (media ± EE) que caracterizan los microhábitats disponibles y utilizados por H. quadrileneatus *(Hq) y* H. festivus *(Hf) en dos tipos de ecosistema (la playa y el bosque).*

	Beach		Forest		
	Available	Hq	Available	Hq	Hf
	N = 15	N = 25	N = 20	N = 25	N = 33
Substrate					
Sand (%)	84.2 ± 6.3	79.1 ± 5.9	–	–	–
Leaf litter (%)	12.9 ± 6.1	4.5 ± 2.1	88.4 ± 5.2	84.0 ± 3.7	88.3 ± 4.3
Grass (%)	–	10.0 ± 4.7	9.8 ± 4.8	9.2 ± 3.4	4.9 ± 3.1
Bare soil (%)	–	–	0.9 ± 0.7	6.0 ± 1.9	3.9 ± 1.6
Tree trunk (%)	2.9 ± 1.0	6.4 ± 2.2	0.9 ± 0.5	0.8 ± 0.5	2.9 ± 1.2
Dry (%)	47.1 ± 12.3	40.5 ± 9.7	10.0 ± 6.9	76.0 ± 8.7	27.3 ± 7.9
Humid (%)	52.9 ± 12.3	59.5 ± 9.7	90.0 ± 6.9	25.0 ± 8.7	72.7 ± 7.9
Sunny (%)	16.7 ± 8.1	27.8 ± 8.1	2.8 ± 2.8	25.8 ± 6.6	25.8 ± 4.2
Vegetation contacts					
5 cm	3.8 ± 1.9	11.3 ± 3.1	2.5 ± 1.1	4.0 ± 1.1	2.8 ± 0.9
10 cm	9.1 ± 2.1	14.3 ± 3.4	10.9 ± 3.7	10.5 ± 2.5	4.7 ± 1.3
25 cm	12.1 ± 2.3	5.0 ± 1.1	16.5 ± 3.6	4.3 ± 1.2	8.9 ± 1.9
50 cm	5.8 ± 2.1	6.8 ± 1.9	10.3 ± 2.6	1.5 ± 0.7	10.8 ± 2.4
Tree cover (%)	56.3 ± 10.7	11.0 ± 4.4	91.3 ± 5.5	21.3 ± 8.1	99.2 ± 0.8
Vegetation type					
Ipomoea sp. 1	4.6 ± 2.0	16.5 ± 4.4	–	–	–
Ipomoea sp. 2	2.5 ± 1.8	5.3 ± 1.6	–	–	–
Coccoloba	19.2 ± 5.5	13.1 ± 2.4	–	–	–
Hybiscus	3.3 ± 2.2	4.2 ± 1.7	–	–	–
Heliconia	–	–	3.4 ± 1.1	1.3 ± 0.5	7.0 ± 2.2
Rubiaceae	–	–	7.5 ± 2.4	–	7.0 ± 2.0
Piperaceae	–	–	11.3 ± 4.0	–	4.7 ± 1.6
Cyperaceae	–	–	6.6 ± 3.0	16.8 ± 3.6	6.8 ± 2.2
Gramineae	–	–	6.3 ± 3.7	1.3 ± 0.8	0.7 ± 0.5
Palmae	–	–	0.2 ± 0.2	–	0.9 ± 0.6

Interestingly, some of these patterns of microhabitat selection of *H. quadrilineatus* were different in each ecosystem, but the differences in availability did not always seem to explain these shifts in microhabitat use. Thus, higher availability of leaf litter in the forest may clearly explain that *H. quadrilineatus* used microhabitats with more leaf litter here than on the beach. However, *H. quadrilineatus* used dryer substrates with more grass and fewer tall bushes in the forest than in the beach even though the availability of these microhabitats did not change (for bushes) or changed following the opposite pattern (e.g. humidity) between ecosystems. If we consider that the patterns of microhabitat use on the beach (where only *H. quadrilineatus* was found) were optimal for this species, the shifts observed in the forest populations may be explained by the interspecific competition with the sympatric *H. festivus,* which results in a competitive displacement to suboptimal microhabitats. With these shifts in habitat use, there was no ecological overlap in the forest between species in the use of microhabitats regarding grass or bush cover. Similar shifts in habitat use or displacement to sub–optimal microhabitats have been studied in detail in popu-

Table 2. Principal components analysis for variables describing available microhabitats used by *H. quadrileneatus* and *H. festivus* lizards. Correlations in bold lettering correspond to variables significantly correlated with a PC ($p < 0.0001$). Results (F, p) of ANOVAs comparing PC scores between microhabitats available and used by each lizard species are shown.

Tabla 2. Análisis de componentes principales para las variables que describen los microhábitats disponibles y utilizados por los lagartos H. quadrileneatus *y* H. festivus. *Los valores en negrita corresponden a las correlaciones significativas de las variables con un componente principal (PC en su sigla en inglés; $p < 0,0001$). Se muestran los resultados (*F, p*) de los ANOVAS que comparan las puntuaciones de cada PC entre los microhábitats disponibles y los utilizados por cada especie de lagarto.*

Variable	PC–1	PC–2	PC–3	PC–4	PC–5	PC–6
Substrate						
Sand	**–0.36**	0.26	–0.05	0.14	–0.01	0.11
Leaf litter	**0.40**	–0.16	–0.02	–0.12	0.04	–0.07
Grass	–0.08	**–0.37**	0.30	0.14	–0.40	0.01
Bare soil	0.05	–0.29	–0.09	0.03	0.07	0.14
Tree trunk	–0.15	0.13	0.13	–0.12	**0.45**	0.15
Dry	–0.09	–0.18	**–0.34**	0.40	0.30	–0.21
Humid	0.08	0.22	0.33	–0.38	–0.30	0.21
Sunny	0.02	–0.11	0.07	–0.17	–0.05	–0.19
Vegetation contacts						
5 cm	–0.25	–0.21	0.34	0.01	–0.02	–0.16
10 cm	–0.14	–0.23	0.37	0.20	0.04	0.10
25 cm	0.14	0.14	0.25	**0.44**	–0.03	0.14
50 cm	0.20	**0.34**	0.17	0.29	–0.02	–0.17
Tree cover	0.35	–0.16	–0.07	–0.14	0.09	0.12
Vegetation type						
Ipomoea sp. 1	–0.30	0.01	0.27	–0.13	–0.06	–0.25
Ipomoea sp. 2	–0.26	0.05	0.17	–0.17	0.30	0.03
Coccoloba	–0.14	0.21	–0.13	0.28	–0.15	0.40
Hybiscus	–0.15	0.10	–0.04	0.15	–0.27	**–0.47**
Heliconia	0.24	0.07	0.16	0.17	–0.04	–0.03
Rubiaceae	0.27	0.20	0.20	0.01	0.09	–0.26
Piperaceae	0.24	0.16	0.22	0.09	0.23	0.06
Cyperaceae	0.06	–0.41	0.15	0.15	–0.07	0.04
Gramineae	0.11	–0.05	0.18	0.24	–0.07	**0.36**
Palmae	0.02	0.10	0.12	–0.02	**0.60**	–0.08
Eigenvalues	4.32	3.22	2.64	2.07	1.32	1.23
% variance explained	18.8	14.0	11.5	9.0	5.7	5.3
ANOVAs:						
$F_{4,113}$	85.84	18.31	4.75	1.58	0.74	2.75
p	**< 0.0001**	**< 0.0001**	**0.0014**	0.19	0.57	**0.032**

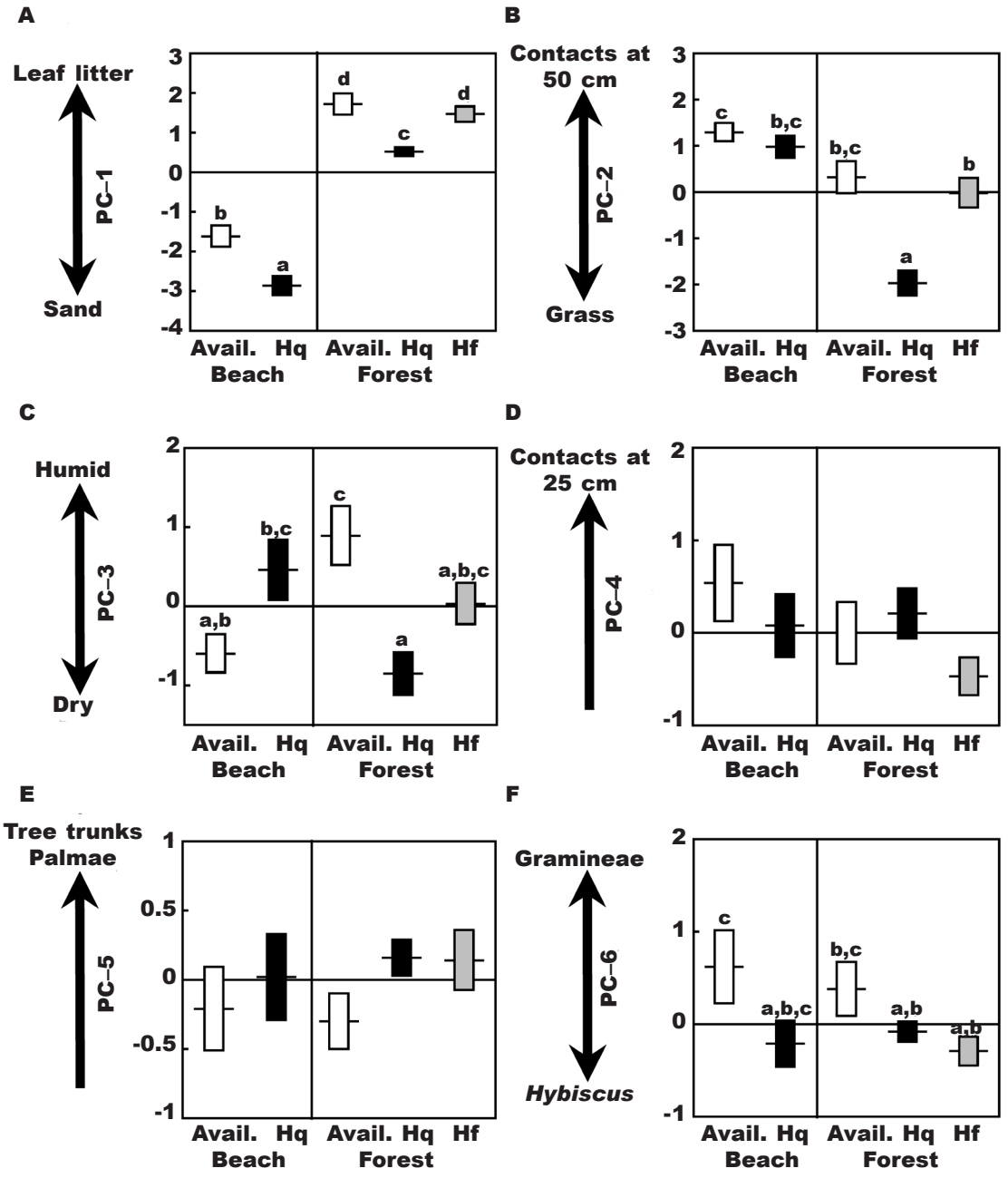

Fig. 2. Mean (± SE) principal component (PC) scores from a PC analysis of all variables describing available microhabitats (open boxes) used by *H. quadrilineatus* (black boxes) and *H. festivus* (grey boxes) in each ecosystem (beach or forest). Means with the same letter above the bars did not differ significantly ($p > 0.05$) in post–hoc pairwise Tukey tests.

Fig. 2. Media (± EE) de las puntuaciones de los PC resultantes de un análisis de componentes principales de todas las variables que describen los microhábitats disponibles (cajas blancas) y los utilizados por H. quadrilineatus *(cajas negras) y* H. festivus *(cajas grises) en cada ecosistema (playa o bosque). Las medias con la misma letra encima no presentaron diferencias significativas* (p > *0,05) en las pruebas de Tukey realizadas para comparar pares de medias a posteriori.*

lations of *Anoli*s lizard species. For example, in the Bermudas*, Anolis leachi* is behaviorally dominant over *A. grahami*, so that *A. grahami* has to use perches of smaller diameter and lower height (Schoener, 1975; Losos, 1996). In this case both species can coexist because the subordinate, *A. grahami*, adapts to habitats unavailable *to A. leachi.* In Gran Cayman Island, the native *A. conspersus* has changed perch height and uses higher perches in open areas where it is sympatric with the introduced *A. sagrei*. In this case, competitive interactions are an improvement for ecological segregation among species (Losos et al., 1993). In another situation, native *A. carolinenesis* uses higher perches when its introduced congeneric competitor *A. sagrei* is present, suggesting that *A. sagrei* displaces the native *A. carolinensis* (Echternacht, 1999; Edwards and Lailvaux, 2012).

As explained above, these differences in the use of microhabitats, which may allow the coexistence of two similar species that could otherwise be potential competitors, may be due to past or current competitive pressures (Schoener, 1975; Medel et al., 1988; Vanhooydonck et al., 2000; Vitt et al., 2000b; Kolbe et al., 2008). Nevertheless, the observed differential use of microhabitats may be a result of the different ecological requirements of each species (Huey et al., 1974: Barbault et al., 1985; Castilla and Bauwens, 1991; Daly et al., 2008). However, if the specific ecological requirements were the only explanation for the microhabitat use of *H. quadrilineatus*, then the same patterns or trends of habitat use would be observed in both types of ecosystems, but we found in contrasting opposite patterns between the forest and the beach in some cases. Other authors argue that the differential use of microhabitats may just be a reflection of differences in habitat availability (Johnson et al., 2006). However, our data showed that differences in availability between ecosystems alone could not explain all the shifts in microhabitat use observed in *H. quadrilineatus*.

Within the forest, however, both species use microhabitats with similar humidity conditions, even though *H. quadrilineatus* used dryer microhabitats here than on the beach, which might reflect that this species was trying to avoid overlap in this factor too. Other microhabitat variables did not differ between species. Thus, there could be competence for some aspects of the microhabitat or these microhabitat factors might not be necessary for the ecological requirements of these lizards. Also, it is essential to consider environmental conditions when examining the existence of interspecific competition because when the availability of a required resource is high, competition between coexisting species may be weak (Paterson et al., 2018).

Previous studies on the specificity of habitat use of both *Holcosus* lizard species indicated that *H. quadrilineatus* uses open areas that have less plant cover and greater sun exposure than *H. festivus*, with this species being found on the edges of forests, less exposed to the sun and at a lower temperature (Hillman, 1969). This finding reinforces our results, since in our study area, *H. quadrilineatus* was found both on the beach and in the forest, whereas *H. festivus* was found only in the forest. The studies carried out by Sebastian–González and Gómez (2012) in the same Reserve indicated that *H. festivus* was also present in small numbers in the beach area, in contrast with our data. This difference may be due to the time of the year or the location (north or south research station) in which the different studies were conducted.

Differences in size related to thermal biology between the two species can play a role in the differential use of habitats. Larger species have slower heating rates, but also a higher risk of overheating due to the slower cooling rate (Rubalcaba et al., 2019; Sebastian–González and Gómez, 2012). Also, larger species maintain higher body temperature for longer due to the lower convective heat dissipation and greater thermal inertia, which makes the loss of heat slower (Carrascal et al., 1992). Therefore, they will have a higher risk of overheating in warm regions (Rubalcaba et al., 2019), and will be forced to select more closed (shady) microhabitats than smaller species. Similarly, in some species of *Sceloporus* lizards, an effect of habitat structure and temperature of the environment has been observed in the selection of microhabitats (Adolph, 1990). Therefore, differences in habitat use might be only a result of differences in size–related thermal ecology. Body size differences can also be decisive in interspecific competition, as larger animals would be dominant (Miller, 1967; Schoener, 1983), displacing the smallest ones (Schoener, 1983; Tokarz, 1985; Losos, 1996; Sacchi et al., 2009). For example, *Liolaemus* lizard species show displacement in the use of microhabitats when they are in sympatry *L. tenius* restricts its microhabitat use (it was found only on trees and high perches) in the presence of *L. pictus*, which is large–bodied (Medel et al., 1988).

Further studies should examine the use of microhabitats of both lizard species in other areas with similar habitats but where they do not coincide to determine whether they continue to use the same microhabitats or differ when they are in sympatry in the same locality. Such findings would reinforce our conclusion that these differences or similarities are due to the current competitive ecological interactions. It would also be of value to study the entire ecological niche (activity, diet, thermoregulation) of each species in situations of parapatry and sympatry, in order to obtain more information on their ecological and biological needs and to determine whether there is competition in any other of these ecological aspects. Finally, behavioral studies testing whether there are aggressive interactions or avoidance behavior would be important to discriminate the mechanisms involved in the competition between these species (Jenssen et al., 1984; Hess and Losos, 1991; Korner et al., 2000; Lailvaux et al., 2012).

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